

## Original Article

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**Author for correspondence:**

André Nel,  
Email: [anel@mnhn.fr](mailto:anel@mnhn.fr)

# The oldest-known Lestidae (Odonata) from the late Eocene of Tibet: palaeoclimatic implications

Guoqing Xia<sup>1</sup> , Daran Zheng<sup>2,3</sup>, Régis Krieg-Jacquier<sup>4</sup>, Qiushuang Fan<sup>1</sup>, Yun Chen<sup>1</sup> and André Nel<sup>5</sup> 

<sup>1</sup>State Key Laboratory of Oil and Gas Reservoir Geology and Exploitation, Chengdu University of Technology, Chengdu, China; <sup>2</sup>Department of Earth Sciences, The University of Hong Kong, Hong Kong Special Administrative Region, China; <sup>3</sup>State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment, Chinese Academy of Sciences, Nanjing, China; <sup>4</sup>Office pour les insectes et leur environnement, Opie-odonates, Guyancourt, France and <sup>5</sup>Institut de Systématique, Évolution, Biodiversité, ISYEB-UMR 7205-CNRS, MNHN, UPMC, EPHE, Muséum national d'Histoire naturelle, Sorbonne Universités, Université des Antilles, Paris, France

**Abstract**

Terrestrial fossils from the Palaeogene of Tibet could help us to better understand the past climate and environment in this area. We herein report a new late Eocene non-marine fossil site from southern Nima Basin, central Tibet, SW China, including abundant insects and fishes. These fossils are similar to those from the late Eocene (~39.5–37 Ma) Lunpola–Nima sediment depo-centres in sharing the dominating aquatic bug *Aquarius lunpolaensis* and cyprinid fishes. *Chalcolestes tibetensis* sp. nov., the oldest representative of the modern family Lestidae, is described. Lestidae were previously only recorded in Western Europe, and the oldest records were from the uppermost Eocene of France and the UK. The present discovery demonstrates that Lestidae already had a broad distribution during the Eocene and probably originated much earlier. The recent representatives of *Chalcolestes* occur in the low-altitude ponds or lakes of Western Palaeartic. Together with the other freshwater fossils in this site, this new discovery indicates a humid climate and low altitude for the Nima Basin and nearby basins in the middle part of the Bangong–Nujiang suture zone.

**1. Introduction**

While the damselfly fossil record has greatly increased during recent years, thanks to the study of the mid-Cretaceous Burmese amber fauna, these are mainly Caloptera Belyshev & Haritonov, 1983 and Coenagrionomorpha Bechly, 1996. The recorded Mesozoic Lestomorpha Bechly, 1996 (= Hemiphlebiidae Tillyard, 1926 + Lestiformia Bechly, 1996) (= Lestoidea Calvert, 1901, *sensu* Dijkstra *et al.* 2014) are mainly Hemiphlebiidae, and three or four Lestiformia in the families Cretacoenagrionidae Bechly, 1996, Perilestidae Tillyard & Fraser, 1938 and Synlestidae Tillyard, 1917. The oldest current records of the highly diverse extant Lestidae are from the Latest Eocene (Nel & Paicheler, 1994; Nel & Fleck, 2014). This family is currently subdivided into Lestinae and Sympecmatinae, the former being diverse and frequently found in the Oligocene and the Miocene lacustrine sediments of Europe, while the latter is known by a *Sympecma* sp. from the Late Miocene of Italy, and *Sympecma incerta* (Piton, 1934) from the Pliocene of France (Cavallo & Galetti, 1987; Nel & Paicheler, 1994). No fossil Lestidae is currently recorded outside of Europe, while the family is cosmopolitan (except Antarctica).

Here we report a new fossil site and describe the oldest-known Lestidae from the late Eocene of Tibet (China), attributing it to the extant Western Palaeartic lestine genus *Chalcolestes* Kennedy, 1920. It demonstrates the very broad distribution of Lestidae during the Eocene and supports its potential greater antiquity, in accordance with its extant distribution. We also discuss the palaeoclimatic implications of the new discovery.

**2. Materials and methods**

The fossils including the well-preserved Lestidae were collected in a new late Eocene deposit in northern Kanggale Hill (NK, 31° 58' 21.38" N, 88° 26' 10.19' E, 4662 m a.s.l.) of the south Nima Basin, which is a large Cenozoic continental basin in central Tibet, SW China (Fig. 1). It is an east–west-trending elongated rift basin resting on a Jurassic–Cretaceous marine succession, situated in the Bangong–Nujiang suture zone formed by the Mesozoic collision of the Lhasa and Qiangtang blocks (Kapp *et al.* 2005, 2007; DeCelles *et al.* 2007a). The fossiliferous strata comprise greyish-green mudstones and calcareous shales, interbedded with mudstones,

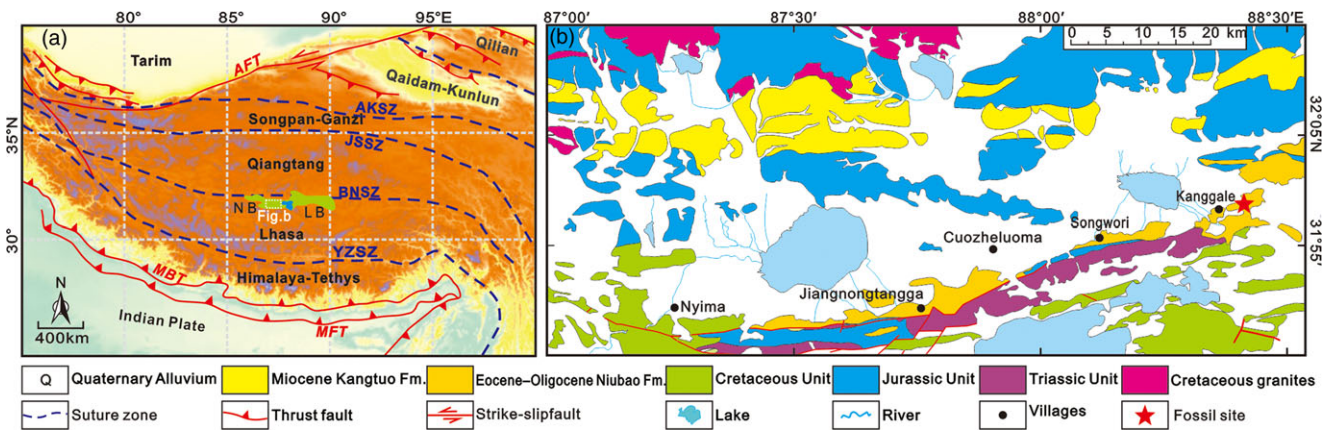


Fig. 1. (Colour online) Geological map showing fossil site in northern Kanggale Hill of Nima Basin, central Tibet, SW China.

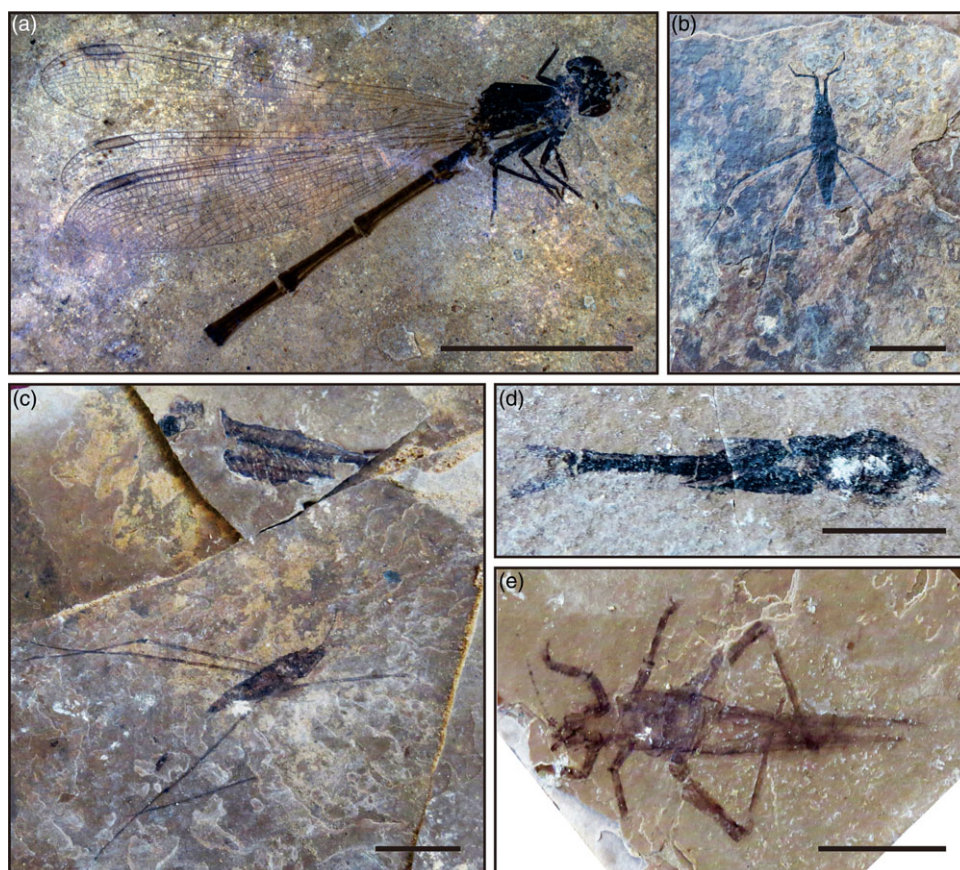


Fig. 2. (Colour online) Photograph showing fossiliferous outcrop in Kanggale Hill.

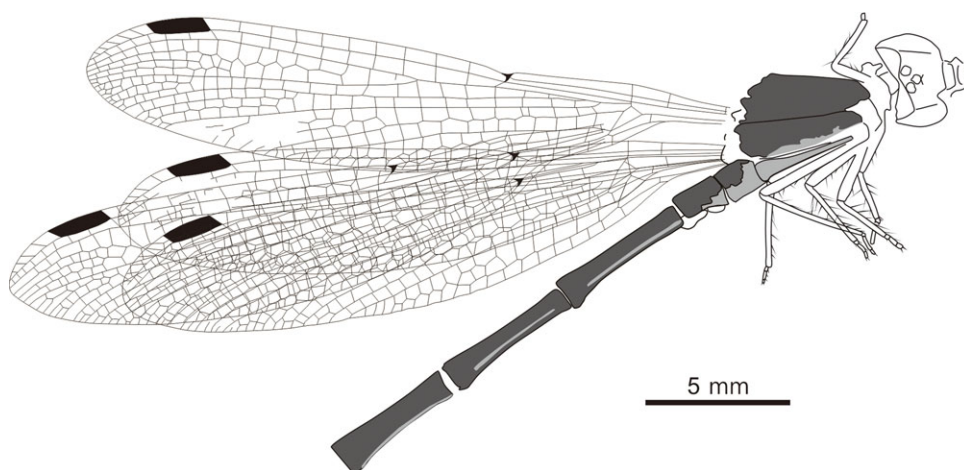
sandstones and limestones (Fig. 2). Abundant fossils including Odonata, Orthoptera, Hemiptera, Hymenoptera and cyprinid fish occur in the greyish-white laminated limestones, dominated by the aquatic hemipteran *Aquarius lunpolaensis* and cyprinid fishes (Fig. 3), previously also recorded in the Dayu area of Lunpola Basin. The latest palaeomagnetic study of the Dayu Section provided a late Eocene (*c.* 39.5–37 Ma) age for the fossil layers (middle Niubao Formation) (Fang *et al.* 2020), thus indicating a late Eocene age for the new fossiliferous layers in the northern Kanggale Hill.

The specimens were examined dry using a Nikon SMZ1000 stereomicroscope. Observation was augmented by temporary wetting with laboratory alcohol, which improved the contrast between the fossil and the matrix, eliminating the surface irregularity of the latter. Photographs were taken using a Canon 5D

digital camera, and line drawings were prepared from these photographs using image-editing software (CorelDraw X8 and Adobe Photoshop CS6). The specimens NIGP 174550 are housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, China. We follow the wing venation nomenclature of Riek & Kukulová-Peck (1984), modified by Nel *et al.* (1993), Bechly (1996, 2016) and Jacquelin *et al.* (2018). Abbreviations. AA, Analis anterior; AP, Analis posterior; Arc, arculus; Ax, primary antenodal cross-vein; C, Costa; CuA, Cubitus anterior; CuP, Cubitus posterior; dc, discoidal cell; IR, Interradius; MA, Media anterior; MP, Media posterior; N, nodus; Pt, pterostigma; RA, Radius anterior; RP, Radius posterior; Rspl, radial supplementary longitudinal vein; sdc, subdiscoidal cell; sn, subnodus.



**Fig. 3.** (Colour online) Representative fossils from fossiliferous outcrop in Kanggale Hill. (a) *Chalcolestes tibetensis* sp. nov., holotype (NIGP174550). (b) *Aquarius lunpolaensis* (Hemiptera). (c) *Aquarius lunpolaensis* and a cyprinid fish. (d) Cyprinid fish. (e) Orthoptera: Grylloidea. Scale bars = 10 mm.



**Fig. 4.** Line drawing of *Chalcolestes tibetensis* sp. nov., holotype (NIGP174550).

### 3. Systematic palaeontology

Order Odonata Fabricius, 1793  
 Family Lestidae Calvert, 1901  
 Genus *Chalcolestes* Kennedy, 1920  
*Chalcolestes tibetensis* sp. nov.  
 (Figs. 3a, 4 and 5).

Material. Holotype NIGP174550; imprint of a body with attached legs and wings, only five abdominal segments preserved; head deformed by the compression, so that the eyes seem to be closer than in an extant Lestidae, as occurs frequently for compression fossil damselflies; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, China.

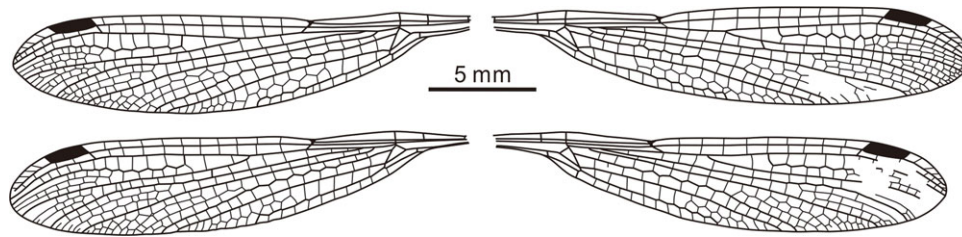


Fig. 5. Line drawing of four wings of *Chalcolestes tibetensis* sp. nov., holotype (NIGP174550).

**Etymology.** Named after the Tibet region where the type was found.

**Age and outcrop.** Late Eocene; Kanggale Hill, south Nima Basin, Central Tibet, China.

**Diagnosis.** Wings *c.* 21 mm long; only ten postnodal cross-veins; pterostigma covering two cells; base of AA clearly basal to CuP; five to six cells in supplementary row between MP and CuA in forewing and three rows in hind wings.

**Description.** Body length *c.* 17 mm, head length *c.* 1 mm, thorax length *c.* 3 mm and abdominal length *c.* 13 mm; head dark, broader than long. Eyes not well preserved, separated by gap of 0.8 mm. One foreleg, two mid-legs and two hind legs preserved (Fig. 3). Left forewing complete (Fig. 4). Wing length 21.2 mm; length from wing base to Arc 3.3 mm, from Arc to N 4.1 mm, from N to Pt 9.9 mm, from Pt to wing apex 3.8 mm. Primary antenodal cross-veins preserved, Ax0 close to wing base, Ax1 1.9 mm distal of Ax0, Ax2 1.3 mm distal of Ax1; no secondary antenodal and antesubnodal cross-veins present. Ten postnodal cross-veins nearly aligned with ten postsubnodal cross-veins present before Pt. Four postnodal and six postsubnodal cross-veins present distal of Pt, non-aligned. Arc aligned with Ax2. dc basally closed, free with strong distal angle; length of basal side 0.6 mm, of anterior side 0.3 mm, of distal side 0.8 mm, of posterior side 1.2 mm. sdc free and elongate, 1.7 mm long and maximum 0.3 mm wide. CuP 0.3 mm distal of level of Ax1. Nodal structures well preserved, Sn aligned with Cr. Midfork (base of RP3/4) lying closer to dc than to Arc, and 1.0 mm distal of Arc. Base of IR2 one cell and 0.6 mm distal of midfork. RP2 originating three cells distal of Sn, lying 3.0 mm distally, nearer to N than to Pt. IR1 long, originating two cells distal of base of RP2 and six cells basal of Pt, lying 2.7 mm distal of base of RP2; one row of cells present between IR1 and RP1, and three cells between IR1 and RP2. Rspl well present, with one row of cells between it and IR2, MA distally zigzagged and long. MP long and slightly curved, with one or two rows of cells between it and CuA. CuA long, with one row of cells between it and posterior wing margin. Pt long, hyaline, covering two cells and well braced, 2.0 mm long and 0.5 mm wide; posterior side of Pt thickened and fused with strongly thickened pterostigmal part of RA to form U-shaped structure; Pt brace in same oblique with Pt base.

#### 4. Discussion

##### 4.a. Relationship between *Chalcolestes tibetensis* sp. nov. and Lestidae

The wing venation of *Chalcolestes tibetensis* sp. nov. is characteristic of the Lestidae and more precisely of the subfamily Lestinae, because of the elongate pterostigmata; bases of RP3/4 and IR2 midway between arculus and nodus; an oblique cross-vein 'O'; distal discoidal vein MAb very oblique, with distal angle of

discoidal cell very acute; MA strongly zigzagged; area between IR2 and RP3/4 distally strongly widened with three rows of cells between these two veins; fore- and hind-wing discoidal cells of the same width and shape (excluding the Sympecmatinae Fraser, 1951 that have discoidal cell in forewings narrower and shorter than in hind wings); arculus mainly formed by the basal discoidal cross-vein, so that the discoidal cell is nearly touching the RA.

The Eocene *Eolestes syntheticus* Cockerell, 1940 (type species of the Eolestidae Greenwalt & Bechly, 2014) and *Chalcolestes tibetensis* sp. nov. have similar wing venations especially in the base of AA quite basal to CuP and the presence of secondary rows of cells between MP and CuA, but with the following major differences: area between RP3/4 and IR2 distally strongly widened with three rows of cells between these veins in *C. tibetensis* sp. nov. (as in other Lestidae); MA more strongly zigzagged in *C. tibetensis* sp. nov. as in other Lestidae; and pterostigma clearly shorter in *C. tibetensis* sp. nov. than in *Eolestes*. The synlestid genus *Megalestes* has a venation similar to those of the Lestidae and of *C. tibetensis* sp. nov., but differing in the absence of the oblique vein 'O' (although a rudimentary one can be present in some specimens) and clearly less acute distal angle of the discoidal cell with a longer anterior side of the same cell (Münz, 1919: pl. 7, fig. 39; Payra et al. 2021). The enigmatic Eocene taxon *Lutetialestes uniformis* Greenwalt & Bechly, 2014 (in Lestinoidea Calvert *sensu* Bechly, 1996, but of uncertain family) shares with *C. tibetensis* sp. nov. the base of AA quite basal to CuP and the presence of secondary rows of cells between MP and CuA, but differs from it in the MA very weakly zigzagged and ScP less oblique.

Within the Lestidae, the three sympecmatine genera *Sympecma* Burmeister, 1839, *Indolestes* Fraser, 1922 and *Austrolestes* Tillyard, 1913 (incl. *Ceylonolestes* Kennedy, 1920) have the discoidal cell of the hind wing of different shape than that of the forewing, more than 1.15 times, usually 1.3–1.5 times, longer than that of the forewing (Fraser, 1933; Watson & Moulds, 1979; Seehausen, 2017). *Austrolestes* also has the sectors of arculus not appressed to RA (Tillyard, 1913: 422, fig. 2).

The classification of the Lestinae has been the subject of numerous changes in the past. Numerous genera, considered as valid by Fraser (1951), were put as subgenera of *Lestes* by Pinhey (1980), viz. *Chalcolestes*, *Paralestes* Schmidt, 1951, *Xerolestes* Fraser, 1951, plus the three subgenera *Pseudochalcolestes* Pinhey, 1980, *Icterolestes* Pinhey, 1980 and *Malgassolestes* Pinhey, 1980. Pinhey (1980) synonymized the subgenus *Africalestes* Kennedy, 1920 with the subgenus *Lestes*. Vajda et al. (2018) re-separated *Chalcolestes* from *Lestes* on the basis of body characters of adult and nymph. After Fraser (1951), the vein AA separating from AP distinctly basal to vein CuP is a character proper to the genus *Chalcolestes*, vs AA emerging at the level of CuP or even slightly more basal in the other Lestinae (see also Tillyard, 1913: fig. 1). This character is present in *Chalcolestes tibetensis* sp. nov. and even

more pronounced than in the two extant species *Chalcolestes parvidens* (Artobolevsky, 1929) and *C. viridis* (Van der Linden, 1825). Nevertheless, Jödicke (1997) indicated that not all specimens of *C. viridis* have this character, rendering it weaker than supposed by Fraser (1951). *C. tibetensis* sp. nov. further differs from these two species in the presence of two rows of —five to six cells in the forewings, and three cells in the hind wings, between MP and CuA.

We investigated the potential affinities of *Chalcolestes tibetensis* sp. nov. with the other lestine genera. *Archilestes* Selys-Longchamps, 1862 (including *Superlestes* Williamson, 1921) has a very broad pterostigma, and the base of RP2 only one cell distal to subnodus, unlike *C. tibetensis* sp. nov. (Münz, 1919: pl. 7, fig. 40; Williamson, 1921; Fraser, 1951; Pérez-Gutiérrez, 2012). *Cyptolestes* Williamson, 1921, synonymized with *Archilestes* by Gloyd (1980), but considered by Donnelly (1981) as a subgenus of *Archilestes*, has a shorter pterostigma than the other species of *Archilestes*. Nevertheless, both also differ from *C. tibetensis* sp. nov. in the more numerous postnodal cross-veins (more than 12 instead of 9–10) (Williamson, 1921). *Superlestes* also has the apex of IR2 opposite the base of the pterostigma.

*Platylestes* Selys-Longchamps, 1862 has a pterostigma quadrate or subquadrate (Münz, 1919). *Icterolestes* has a short pterostigmata (1.5 mm or less, vs 2.0 mm in *Chalcolestes tibetensis* sp. nov.) and wing apices rounded instead of being acute in *C. tibetensis* sp. nov. (Pinhey, 1980). *Sinhalestes* Fraser, 1951 has 18–20 postnodal cross-veins, unlike *C. tibetensis* sp. nov. (Fraser, 1933). *Orolestes* McLachlan, 1895 has a longer pterostigma, covering more than four cells, and the wings of males broadly banded or spotted with brown colour (McLachlan, 1895; Martin, 1903; Fraser, 1951). The *Lestes* subgenera *Paralestes* and *Malgassolestes* have only long intercalary veins in the area between MA and RP3/4, unlike *C. tibetensis* sp. nov. (Fraser, 1951; Schmidt, 1951; Pinhey, 1980). *Pseudochalcolestes* differs from *C. tibetensis* sp. nov. in the base of AA opposite CuP in hind wing and the presence of only one supplementary longitudinal vein between MA and RP3/4 (Schmidt, 1951). *Xerolestes* differs from *C. tibetensis* sp. nov. in the longest intercalary vein between RP3/4 and MA beginning well basal to base of RP2 (Pinhey, 1980). The subgenus *Lestes* differs from *C. tibetensis* sp. nov. in the base of AA opposite CuP in fore- and hind wing.

Several fossils currently attributed to *Lestes* with a supplementary row of cells in the area between MP and CuA are known from the latest Eocene and Oligocene in Europe. We need to compare *Chalcolestes tibetensis* sp. nov. to these taxa. *C. tibetensis* sp. nov. has a wing venation very close to that of the latest Eocene *Lestes regina* Théobald, 1937 (Gard, France), even in the wings' sizes (20–22 mm long in *L. regina* and 22 mm in *C. tibetensis* sp. nov.), but the latter has 11–12 postnodals, four cells between subnodus and base of RP2 and 5–6 cells in the supplementary row between MP and CuA in all wings (Théobald, 1937; Jattiot *et al.* 2020). Nel & Fleck (2014) described a latest Eocene fossil as *Lestes* aff. *regina* (Isle of Wight, UK), very similar to the French fossils. The early Oligocene *Lestes forsterii* Hess, 1895 (Haut-Rhin, France) and *L. vicina* Hagen, 1858 (Germany) have five cells in the supplementary row between MP and CuA but 11–12 postnodal cross-veins (Hagen, 1858; Théobald, 1937). The Oligocene *Lestes ceresti* Nel, 1985 (Vaucluse, France) also has a venation very close to that of *C. tibetensis* sp. nov., but many more cells in the supplementary row between MP and CuA (8–12 cells), more postnodal cross-veins and longer wings

(25.2–28.8 mm long) than *C. tibetensis* sp. nov. It seems that the base of AA and CuP are closer to each other in *L. ceresti* than in *C. tibetensis* sp. nov. (Nel & Papazian, 1985; Nel & Paicheler, 1994;). The Oligocene *Lestes brisaci* Nel *et al.* 1997 (Vaucluse, France) has only two to four cells in the supplementary row between MP and CuA, but four cells between subnodus and base of RP2 (Nel *et al.* 1997). The Oligocene *Lestes statzi* Schmidt, 1958 (Germany) has many more postnodals than *C. tibetensis* sp. nov., base of RP2 three to four cells distal of subnodus, and only one to three cells in the supplementary row between MP and CuA (Schmidt, 1958). The latest Oligocene *Lestes aquisextana* Nel, 1985 has only one cell in the same area but two rows of cells between CuA and posterior wing margin (Nel, 1985; Nel & Paicheler, 1994).

In the sister clade (Synlestidae + Perilestidae) of the Lestidae, the base of AA is well basal to CuP in *Megalestes* (see Gyeltshen *et al.* 2017; Payra *et al.* 2021) while AA separates from AP quite distal to CuP in *Synlestes* and *Nubiolestes* and there is no distinct AA in *Perilestes* (Münz, 1919; Schmidt, 1942). But as *Megalestes* is the sister group of all the others (Synlestidae + Perilestidae), it is likely that the situation in this genus is plesiomorphic, while the other representatives of this clade have a strong tendency to pronounced petiolation with a distal 'migration' of AA. The presence of the same situation in *Hemiphlebia mirabilis* (Hemiphlebiidae, sister group of all other Lestomorpha) supports this hypothesis. Also, the Early Cretaceous *Cretalestes martinae* Jarzembowski *et al.* 1998 and two Eocene taxa *Eolestes syntheticus* and *Lutetialestes uniformis* have the base of AA well basal to CuP, suggesting that it is the plesiomorphic state of character for the Lestoidea. *Chalcolestes* would have kept this state of character. Thus, the attribution of *C. tibetensis* sp. nov. to this genus is based on a plesiomorphy, rendering it only tentative. Nevertheless, without other evidence to the contrary and any autapomorphic character that would allow the creation of a new lestid genus, we prefer to keep it in this genus. Also a phylogenetic analysis of the whole Lestidae is necessary to clarify the relationships in this family.

The synlestid genus *Megalestes* has a venation very similar to those of the Lestidae and *Chalcolestes tibetensis* sp. nov., but differing in the absence of oblique veins 'O' and clearly less acute distal angle of the discoidal cell with a longer anterior side of the same cell (Münz, 1919: pl. 7, fig. 39).

#### 4.b. Remarks

Jattiot *et al.* (2020: 435) indicated that a 'supplementary row of cells between MP and CuA can be found also in some specimens but not in others, of extant *Lestes* species (*L. dryas* Kirby, 1890)', but it is remarkable that a majority of Lestinae from the Eocene and Oligocene share this character, while those from the Miocene have only one row of cells in this area. This character is also rare among the extant Lestinae. This phenomenon needs further material to be confirmed, but the present discovery of *Chalcolestes tibetensis* sp. nov. is one more case supporting it. The presence of the same character in the two Eocene *Eolestes syntheticus* and *Lutetialestes uniformis* would suggest that it could also be a plesiomorphy in the Lestiformia, but this hypothesis needs to be confirmed because the Hemiphlebiidae do not share it.

### 5. Conclusion

#### 5.a. Fossil calibration

*Chalcolestes tibetensis* sp. nov. is the oldest record of the crown group of Lestidae, as the previous ones were from the Latest

Eocene of France and the UK (33.9–28.4 Ma). The widespread distribution of this family during the Eocene suggests a greater antiquity. Unfortunately, the putative older record of *Lestes zaleskyi* Piton, 1940 from the Palaeocene of Menat (France) is very uncertain because its original description is very imprecise and the holotype is lost (Nel & Paicheler, 1994: 7).

### 5.b. Palaeoclimatic implications

The modern-day hinterland of the Tibetan Plateau has a relatively low-relief topography, in stark contrast to the high-relief Himalaya and surrounding mountain ranges (Fielding et al. 1994); such a unique low-relief landscape in central Tibet has been formed since at least the late Eocene (Han et al. 2019). The Palaeogene Lunpola–Nima sediment depo-centre is located between the palaeo-Gangdese and the palaeo-Qiangtang (Tangulha) mountain ranges to the south and north of the basin (DeCelles et al. 2007b), respectively. It is generally accepted that Qiangtang Block in the north entered into collision by the Cretaceous and has since been in an intracontinental setting (Yin & Harrison, 2000). The Gangdese Mountains in the south have probably also maintained high elevations since at least the Palaeocene (Ding et al. 2014). However, the Palaeogene topographic characteristics and palaeoclimatic history of the Lunpola–Nima sediment depo-centre between the palaeo-Gangdese and the palaeo-Qiangtang (Tangulha) mountains are very poorly known.

Some isotope studies suggest a high Lunpola Basin floor (4–5 km) (Rowley & Currie, 2006; Decelles et al. 2007b; Polissar et al. 2009; Quade et al. 2011), a high palaeo-Gangdese (~4.5 km; Ding et al. 2014) and a high palaeo-Qiangtang/Tangulha mountain range (>5.0 km; Xu et al. 2013; Lin et al. 2020). However, evidences from palaeobotany (Wang et al. 2018) and palaeontology (Deng et al. 2011; Sun et al. 2014; Ma et al. 2017; Wu et al. 2017; Su et al. 2019) suggest much lower elevations (1–3 km). Moreover, emerging numerical simulations of palaeoelevations based on temperature constraints and thermal lapse rates are also widely divergent (e.g. Botsyun et al. 2019; Valdes et al. 2019). In view of this situation, the fundamental reason for the contradiction of the above-mentioned palaeoelevation reconstruction results is that the stratigraphic age of the Lunpola basin has not been well constrained (Fang et al. 2020). In other words, the high altitude of the Lunpola Basin proposed by Rowley & Currie (2006) mainly refers to the late Oligocene period of 26.5–23.3 Ma, while palaeontological teams proposed that the low elevation was mainly for the Eocene period of 39.7–37 Ma (Wu et al. 2017; Su et al. 2019). Most importantly, after the comprehensive study of a large number of plant fossils by Su et al. (2020), a subtropical forest called the ‘Shangri La’ ecosystem was also proposed for the Middle Eocene (~47 Ma). Its palaeogeomorphological features are low valleys distributed in an east–west direction, at ~1500 m elevation within an east–west-trending valley under a monsoonal climate with a mean annual temperature of ~19 °C and a cold-month mean temperature of  $7 \pm 2.9$  °C with rare frosts.

Our finding provides evidence for a regional climate system and its possible response to Tibetan landscape evolution. The steady specific ecosystem directly affects insect population dynamics and geographic distributions. As ectotherms, insects are highly sensitive to ambient temperatures and may respond very quickly to temperature fluctuations (Robinet & Roques, 2010). The recent *Chalcolestes parvidens* and *Chalcolestes viridis* have Western Palaeartic distributions (Southern, Eastern and Central Europe,

Syria, Jordan, Israel, Turkey, and Maghreb in North Africa), all under low altitudes (Wildermuth & Martens, 2019). *Chalcolestes viridis* has a rather narrow temperature tolerance between 14 °C and 24 °C (Romero, 1988). They occur in still or slow-flowing water in ditches, ponds, lakes and canals. The discovery of a *Chalcolestes* in the late Eocene of Tibet indicates a low altitude for the Nima basin during this period and further suggests that the genus is quite old and was more widespread during the Palaeogene.

This conclusion enables us to have a clearer understanding of the palaeogeomorphological constraints of the Nima and the surrounding Lunpola basins during the Palaeogene: the Tibetan landscape comprised a high (>4 km) Gangdese mountain range along the southern margin of the Lhasa terrane and a Tangulha upland on the more northerly Qiangtang terrane; while the Nima, Lunpola and other basins in the middle of the Bangong Nuijiang suture zone were almost in the valley area, with relatively low altitudes, c. 1500– m a.s.l.

This discovery provides a warm and humid climate with low latitude for the Niima and Lunpola basins during the late Eocene.

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**Conflict of interest.** We declare that we have no conflict of interest.

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